

Spatiotemporal heterogeneity of the palaeoecological record in a large temperate palaeolake, Šúr, southwest Slovakia: Comparison of pollen, macrofossil and geochemical data

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ABSTRACT

Aquatic macrophytes living within shallow lakes are particularly sensitive to climate change and fluctuations in water depth. In the Dabubian Lowland of southwestern Slovakia, sediments from the large, shallow palaeolake, named Šúr, provide a unique opportunity to reconstruct changes in water depth to analyse succession within local aquatic and terrestrial vegetation. Here, we used a multi-core, multi-proxy approach (macrofossils, pollen, and geochemistry) in order to reconstruct water depth changes and its influence on aquatic and terrestrial vegetation succession during the Holocene. Additionally, we also consider how heterogeneity in proxy data varied across time and space. Using particular macrophyte taxa found in the macrofossil assemblage, which have specific water depth requirements, our results demonstrate changes in water depth created a long-term mosaic of vegetation succession. In the Early Holocene, aquatic macrophytes suggest the water column was high (> 100 cm). During the Middle Holocene, water depths decreased creating mosaics of aquatic succession. By ca 4200 cal yr B.P., terrestrialization had occurred in the former lake area. Regional vegetation succession was likely more influenced by the presence of fluvial sands and/or by low precipitation and high evaporation rates, which delayed the expansion of temperate trees and favoured *Pinus* until 8850 cal yr B.P. Macrofossils exhibit the lowest temporal variation among all proxies, which suggests a rather stable macrophyte community when water depth was high. Pollen data show very low spatial variation given by the size of the accumulation basin, which reflects regional pollen rain. Higher spatial variation was observed in the geochemistry and macrofossil data compared to the pollen data, which could be the result of different mosaics of aquatic plants, local dispersion of propagules, or changes in sediment types. We conclude that changes in water depth were not homogenous, but rather heterogeneous in space and time.

1. Introduction

Lake sediments provide various types of biotic and abiotic proxy data and are therefore considered lake archives (Cohen, 2003). Studying several types of proxy data (e.g. macrofossils, pollen and geochemical composition) obtained from limnic sediments provides a complex view of the past local environment of the lake and its catchment area (Birks and Birks, 2006; Birks et al., 1996). Even though, in European lowlands lake deposits are very common in deglaciated regions, where numerous lakes of glacial origin occur, however lakes are rather scarce in non-glaciated regions. Every lake sedimentary basin in

a non-glaciated region represents an important source of palaeolimnological information relevant to a relatively large area. It is therefore desirable to examine as many types of palaeoecological proxy data as possible, and with respect to the actual lake basin area, also an adequate number of cores, to exploit the full potential of limnic sediments.

The Pannonian Basin (also known as the Carpathian Basin) was never glaciated during the Quaternary period (Ehlers and Gibbard, 2004). Shallow and saltwater lakes located in the Pannonian Basin are typically found in tectonic depressions (e.g. Fehér, Fertő, Bőddi-szék, Kelemen-szék), or were formed during the Last Glacial by Aeolian sand

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formations (Hájková et al., 2015; Ujházy et al., 2003) or by fluvial activity (Magyari et al., 2008). Previous palaeolimnological research in the Western Pannonian Basin has focused mainly on the largest Central-European lake, Lake Balaton (Medzihradský, 2005; Sümegei et al., 2008; Korponai et al., 2010) as well as on lakes in southern Moravia (Vracov palaeolake - Rybníčková and Rybníček, 1972; Svobodová, 1997; Kuneš et al., 2015 and Čejč palaeolake - Břizová, 2009). The Danubian Lowland, situated on the border of the Western Pannonian Basin and the Western Carpathians, has, from a palaeolimnological perspective, been almost neglected until recently (but see Pišút et al., 2010; Petr et al., 2013).

We therefore decided to focus on organic deposits of the palaeolake Šúr, located in the Danubian Lowland (SW Slovakia), and to reconstruct the past vegetation succession of the lake and the surrounding environment. To examine the complexity of the past long-term development of a large lake and to detect past water-depth fluctuations, it is essential to investigate several cores from one lake basin (Harrison and Digerfeldt, 1993; Gaillard and Digerfeldt, 1991; Wasylukowa and Walanus, 2004). However, we are still lacking a palaeolimnological investigation in the area of the Pannonian Basin that would compare several cores from a single lake basin and infer differences in the timing of succession in various parts of a lake. We therefore sampled three cores from the lake basin and examined the nature of sediments, their geochemical composition, macrofossils and pollen to reconstruct past local and regional vegetation development.

The extent of limnic sediments and the presence of the entire Holocene record also provide an excellent opportunity to investigate the variability of the palaeolimnological record. Multi-proxy studies, which deal with several cores from one lake, lack information on how exactly are different proxies influenced by time and space within same lake basin and focus only on the reconstruction of the past environment or climate (e.g. Pokorný and Jankovská, 2000). We therefore decided to quantify the spatial and temporal variability of the palaeorecord in order to contribute to the understanding of the structuring of multi-proxy data in a large shallow temperate lake.

The main goals of the present paper are 1) to reconstruct water-depth fluctuations and the long-term vegetation succession of the palaeolake Šúr, 2) to reveal regional vegetation development, and 3) to compare particular proxies with respect to their temporal and spatial structuring.

2. The study site

The Šúr National Nature Reserve (128–132 m a.s.l.) is situated in a tectonic depression below the southeastern slopes of the Malé Karpaty Mts (Little Carpathian Mts), near the village of Svätý Jur (Fig. 1). The reserve is located in the Podunajská nížina (Danubian Lowland), which is the driest (mean annual precipitation < 500–600 mm) and warmest (mean annual temperature > 10–9 °C) region of Slovakia (mean values are calculated from long time series measured in the time period of 1961–1990; <http://geo.enviroportal.sk/atlassr>). Bedrock consists of clay, gravel and loamy sand flushed down from adjacent slopes during the Pleistocene and Holocene (Slobodník and Kadlečík, 2000).

The Šúr NNR protects the largest alder carr forest in Central Europe and patches of Pannonian thermophilous oak grove vegetation. The present-day vegetation is dominated by tall-trunk alder carr forest (phytosociological association *Carici elongatae-Alnetum glutinosae* Tüxen 1931). At the site numerous endangered plant species still survive, examples being *Urtica kioviensis*, *Thelypteris palustris*, *Hydrocharis morsus-ranae* and *Hottonia palustris* (Füry, 2010). The Šúr locality was declared as a wetland of international importance and was included under the Ramsar convention in 1990 and then on the list of NATURA 2000 habitats (Füry, 2010).

The site was surveyed comprehensively in the 1950s due to plans to open a peat mine, which were fortunately abandoned. The locality was examined in detail by manual coring in a grid of 50 × 50 m. Every core

was lithologically described and plotted on a map (Danišovič et al., 1956), which provides an excellent overview of the placement and thickness of deposited organic and inorganic layers in the entire basin (Fig. 1).

The sediments of the palaeolake Šúr were first palynologically investigated by O. Kintzler (1936) and revisited a few years ago by Petr et al. (2013), who analysed one core.

The Šúr basin is supplied by water from several streams flowing from the Little Carpathians and discharges by the Blatina ditch and Čierna voda stream. The entire basin has a high groundwater table, which is illustrated by the presence of extensive pools that cover most of the site during spring snowmelt.

3. Materials and methods

3.1. Coring and laboratory analyses

Three cores were taken in the deepest part of the palaeolake Šúr using a Russian peat corer (5 cm × 50 cm) (Fig. 1) at the following coordinates (WGS-84): Core 1 – N 48°13.893'; E 17°14.156', Core 2 – N 48°13.940'; E 17°13.993', Core 3 – N 48°23.435'; E 17°23.053'. Each core was sub-sampled in the field into plastic bags. The samples were transported to the laboratory and stored in a refrigerator at 4 °C.

For plant macrofossil analyses, samples of 50–100 cm³ volume were used at 5–10 cm resolution. Upper parts of cores containing decomposed peat with low amount of macrofossils were analysed at 10 cm resolution. Sediments were rinsed with water running through 200 and 250 µm mesh sieves. Plant diaspores and other biological remains were picked out from the recovered fraction and examined under a stereomicroscope at a magnification of 12 × and more.

For pollen analyses, samples of 1 cm³ volume were used at 5 cm resolution. Upper parts of cores containing decomposed peat without preserved pollen were not analysed. Samples were processed using standard methods using acetylation by KOH, HCl and HF (Moore et al., 1991). Pollen atlases (Moore et al., 1991; Reille, 1992, 1995, 1998; Beug, 2004) were used for pollen grain identification.

X-ray fluorescence analysis (EDXRF) of geochemical soil properties was carried out at 5–10 cm resolution at the Institute of Inorganic Chemistry at the Czech Academy of Sciences. Sediment samples were analysed after being poured into measuring cells with bottom windows of Mylar foil using a PANalytical MiniPal4.0 spectrometer with a Peltier-cooled silicon drift energy-dispersive detector. Uncalibrated intensities of analytical spectral lines in counts per second (c.p.s.) were used, which they are proportional to elemental concentrations (Grygar et al., 2010).

To estimate the amount of organic carbon in the sediment, LOI (Loss on ignition) analysis at 550 °C was carried out (Heiri et al., 2001). The procedure was conducted according to Petr et al. (2013) to reach comparable results.

3.2. Diagram preparation and data processing

The results of the plant macrofossil, pollen and geochemical analyses were plotted in diagrams using TILIA version 1.7.16 and TILIA.GRAPH (Grimm, 2011). All macrofossil counts were recalculated to a constant sample volume of 50 cm³. The pollen sum in each sample was at least 500 grains. *Alnus* and *Cyperaceae* were excluded from the sum.

We used indirect gradient analysis (NMDS) in Canoco v. 5 (ter Braak and Šmilauer, 2012) to display major patterns of variation in the palaeoecological record.

To estimate the role of temporal development and spatial variability, we partitioned the variance using redundancy analysis (RDA), a multivariate analogue of linear regression. For the analysis, we used only the parts of the cores that overlapped during the estimated time of sedimentation, i.e. 7000–10,500 cal yr B.P. Core identity was used as

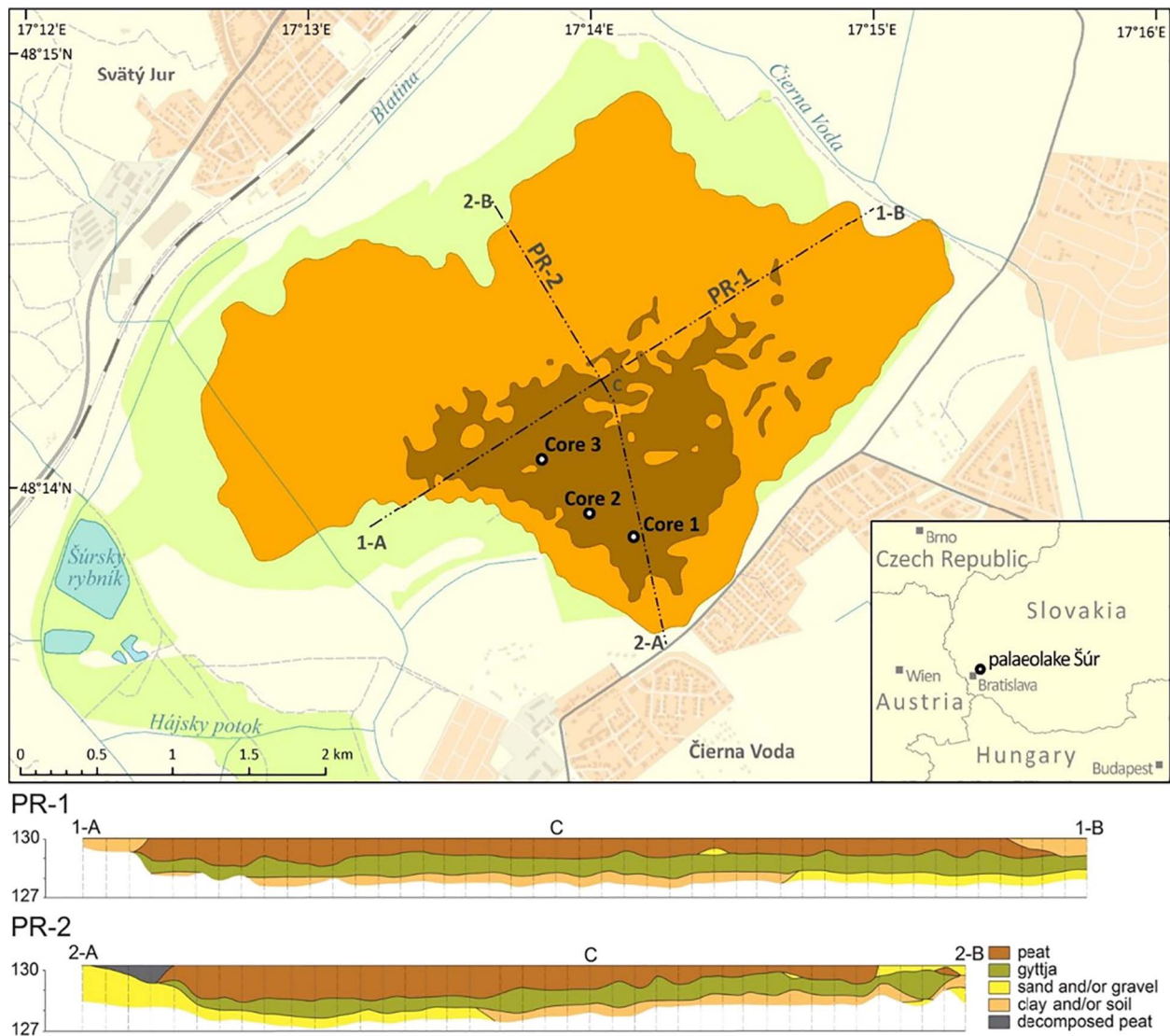


Fig. 1. Map of the lake basin with highlighted thickness of the organic layer (orange: 0–100 cm; brown: 100–200 cm) based on the maps of Danišovič et al. (1956). Cross-section profiles PR-1 and PR-2 depict the thickness and structure of the deposited sediment layers. The left axis represents elevation (m a.s.l.).

the predictor to represent spatial variability, and the estimated sample age was used as the predictor describing temporal dynamics. We estimated the net proportion of the variance explained for each of the predictors after fitting the other one as the covariable. In this way we conservatively estimated the lower bound of the effect, i.e. without the part of the variance that could be ascribed to both predictors. The comparison was based on the adjusted R^2 . We used the “varpart” method from the “vegan” package (ver. 2.3-1, Oksanen et al., 2013) of the R statistical environment (ver. 3.1.1; R Core Team, 2014).

EDXRF counts of 14 elements (Al, Ca, Fe, K, Mn, P, Pb, Rb, S, Si, Sr, Ti, Zn, Zr) were available for all samples. Geochemical data were log-transformed and then standardized to zero mean and unit variance for each of the analysed elements. As regards macrofossil data, we used only those types that were present at least in three samples, which resulted in 31 taxa. The data were Hellinger-transformed before the analysis. The same transformation was used for the pollen data, and again only pollen taxa that were present in at least three samples were used in the analysis (54 taxa).

3.3. Radiocarbon dating and depth-age modelling

A total of 27 samples of biological remains was dated by AMS

radiocarbon analysis at the Centre for Applied Isotope Studies, University of Georgia, USA (Table 1). The radiocarbon dates were calibrated using OxCal 4.2.4 software (Ramsey, 2009), and depth-age was constructed using the Intcal13 atmospheric calibration curve (Reimer et al., 2013). On the basis of a P_Sequence function with a k parameter equal to 1 cm^{-1} , depth-age models with a 1-cm resolution were constructed in Oxcal software. To incorporate into the model the horizons of potential changes in the sedimentation rate, such as contacts between different types of deposits, the command Boundary was applied. In Core 1, boundaries were placed at the depths of 241 cm (sand/gyttja), 198 cm (grey/brown gyttja), 135 cm (gyttja/swamp peat) and 80 cm (swamp peat/woody peat). In Core 2, boundaries were located at depths 146 cm (gyttja/sedge peat) and 110 cm (sedge peat/decomposed peat). In Core 3, boundaries were located at the depths of 175 cm (gyttja/sedge peat) and 130 cm (sedge peat/decomposed peat). In the text below we use mean values of modelled data in the range of 95.4%, rounded to the nearest 50 year step. For the formal subdivision of the Holocene, we followed Walker et al. (2012) with the Early-Middle Holocene boundary at 8200 cal yr B.P. and the Middle-Late Holocene boundary at 4200 cal yr B.P.

Table 1

AMS radiocarbon dating and calibration results. Samples were calibrated using the Oxcal programme (Ramsey, 2009) and IntCal 13 calibration curve (Reimer et al., 2013). Samples marked by asterisks were excluded from age-depth modelling (see Supplementary material).

Lab. code	Depth (cm)	¹⁴ C age (yr B.P.)	Age (cal yr B.P.)	Material
Core 1				
UG-5391	87–90	3220 ± 25	3544–3380	Seeds (<i>Carex</i> sp.)
UG-5589	150–153	4600 ± 25	5448–5146	Seeds (<i>Urtica dioica</i> , <i>Cyperus fuscus</i> , <i>Betula</i> sp.)
UG-5590*	204–207	4360 ± 30	5034–4853	Plant fragments (undeterminable)
UG-7547	210–213	6480 ± 25	7435–7324	Seeds (<i>Betula</i> sp.)
UG-7548	219–222	7250 ± 30	8163–8001	Seeds (<i>U. dioica</i> , <i>Alnus glutinosa</i>)
UG-10528	234–241	9790 ± 60	11,329–10,910	Tree scar (unspecified)
UG-5392*	241–245	25,960 ± 60	30,600–29,841	Charcoal (unspecified)
Core 2				
UG-16127	100–110	2670 ± 60	2925–2717	Nutlets (<i>Carex</i> sp.)
UG-12683	130–135	3500 ± 40	3881–3645	Seeds (<i>U. dioica</i>)
UG-12684	165–170	4470 ± 25	5285–4977	Cone (<i>A. glutinosa</i>)
UG-12685	195–200	6940 ± 30	7839–7689	Bark (unspecified)
UG-12686	220–225	7920 ± 45	8979–8606	Fruits (<i>A. glutinosa</i>)
UG-16128*	230–235	7450 ± 40	8360–8186	Fruits (<i>A. glutinosa</i>)
UG-16129	240–245	8430 ± 45	9530–9320	Fruits, seeds (<i>A. glutinosa</i> , <i>Solanum dulcamara</i>)
UG-16130*	245–250	5020 ± 50	5900–5654	Fruits (<i>Betula</i> sp., <i>C. fuscus</i>), Bryophytes
UG-12687	250–255	12,240 ± 45	14,327–13,985	Fruits (<i>Potamogeton filiformis</i>)
UG-16131*	255–260	1520 ± 105	1816–1175	Fish bones (unspecified)
Core 3				
UG-16132	80–85	4060 ± 70	4821–4416	Seeds (<i>Eupatorium cannabinum</i> , <i>Lemna trisulca</i>)
UG-16133*	130–135	740 ± 35	732–654	Fruits, seeds (<i>A. glutinosa</i> , <i>S. dulcamara</i> , <i>U. dioica</i>)
UG-16134	165–170	6600 ± 30	7679–7364	Cone (<i>A. glutinosa</i>)
UG-16135	205–210	7870 ± 30	8770–8589	Fruits (<i>A. glutinosa</i>)
UG-16136	225–230	8550 ± 45	9583–9470	Fruits (<i>A. glutinosa</i>)
UG-16137*	235–240	Modern	–	Bark (unspecified)
UG-16138*	240–245	8500 ± 85	9660–9300	Catkin scale (<i>Betula</i> sp.)

4. Results and interpretations

4.1. Chronology and age-depth modelling

Using AMS dating, we obtained a sufficient number of dates to create reliable depth-age models, even if some dates were reversed (see Supplementary material). Movement of water or fish activity in the lake might be the reason behind these reversed dates. Two dates were distinct outliers in Core 1 (UG-5392, UG-5590), three dates in Core 2 (UG-16131, UG-16130, UG-16128) and two dates in Core 3 (UG-16138, UG-16133). The outliers significantly decreased the Agreement index of the depth-age model (Amodel) to approximately 0 (values below 60% are treated as thresholds of reliable models; Ramsey, 2008). After the exclusion of outliers, the Amodel reached the values of 96% for Core 1, 100% for Core 2 and 96% for Core 3. Error values varied mostly between 30 and 200 years, being higher only in some, mostly lower parts of cores (Core 1: 200–400 years in 240–180 cm; Core 2: 340–780 years in 251–243 cm; Core 3: 200–300 years in 255–245 cm, in 145–95 cm and in 75–15 cm).

4.2. Sedimentology and changes in geochemical composition (Fig. 2)

For a detailed stratigraphic description, see Table 1 in the Supplementary material. During the Early Holocene, limnic sediment gyttja had accumulated in the lake (Fig. 1). Ti, Si and Fe were very abundant in all three profiles whereas P, S and especially Ca had only low amounts. The high amount of Si indicates that diatoms (their frustules are composed of almost pure silica) were the most important part of the limnic sediment (gyttja), which was confirmed by diatom analysis in Core 1 (Petr et al., 2013). The amount of Fe is associated with the silicate fraction in the sediment and thus covaries with the amount of Si (Bilali et al., 2002). Ti decreased during the Early Holocene, yet the timing differed between particular profiles. Titanium started to decrease at 9500 cal yr B.P. in Core 1, but in Cores 2 and 3 it occurred later, around 8850 cal yr B.P.

The Middle Holocene was characterized by the deposition of gyttja

sediment and high quantities of Si, medium amounts of Fe, Ti, P and S and low amounts of Ca in Cores 1 and 2. Accumulation of gyttja suggests the development of the lake, which continued to accumulate until 3800 and 4200 cal yr B.P. in Core 1 and Core 2, respectively when Si, Fe and Ti curves also declined. The accumulation of gyttja differed in Core 3, which ceased around 7200 cal yr B.P. and subsequently started to accumulate a carbon rich marsh peat, which signals the terminus of lake development. This indicates earlier terrestrialization around 7200 cal yr B.P. in the Core 3. The amounts of Si, Fe and Ti also declined at 7200 cal yr B.P. and remained low throughout the Middle Holocene. By contrast, the amount of S and Ca reached the highest values in the Middle Holocene in Core 3. Ca tends to occupy adsorption sites on organic particle surfaces and thus co-varies with the amount of carbon in the sediment (Oldfield et al., 2003). Organic matter (LOI) was low during the lake developmental phase (i.e. when gyttja was accumulating up to ca 3800 and 4200 cal yr B.P. in Cores 1 and 2, up to ca 7200 cal yr B.P. in Core 3), reaching maxima exceeding 40% in the wetland phase (decomposed marsh peat) reaching up to 80% (Fig. 3).

At the beginning of the Late Holocene (between 3800 and 4200 cal yr B.P.), rapid decreases of Si, Fe and Ti counts were recorded in Cores 1 and 2, reflecting the terrestrialization at these sites. Sediments completely changed in all the cores once the lake was completely filled with peat, which was characterized by the lowest values of Ti, Si and Fe, and by elevated organic matter content (LOI, Fig. 3), S, P and Ca. Organic marsh peat sediment is enriched with sulfur (Oldfield et al., 2003), and its decline in the decomposed peat in the uppermost part of the profile is probably caused by allochthonic minerogenic input to the lake, also indicated by increasing Ti and Si. Allochthonic input indicates erosion runoff, the most pronounced in Core 3 located nearest to the adjacent Little Carpathian slopes. The elevated amount of phosphorus may be linked to the accumulation of *Alnus glutinosa* leaf litter, which has low biodegradability (Krevš et al., 2013) and can be subsequently buried in the sediment together with phosphorus, which is adsorbed onto organic particles (Busse and Gunkel, 2002).

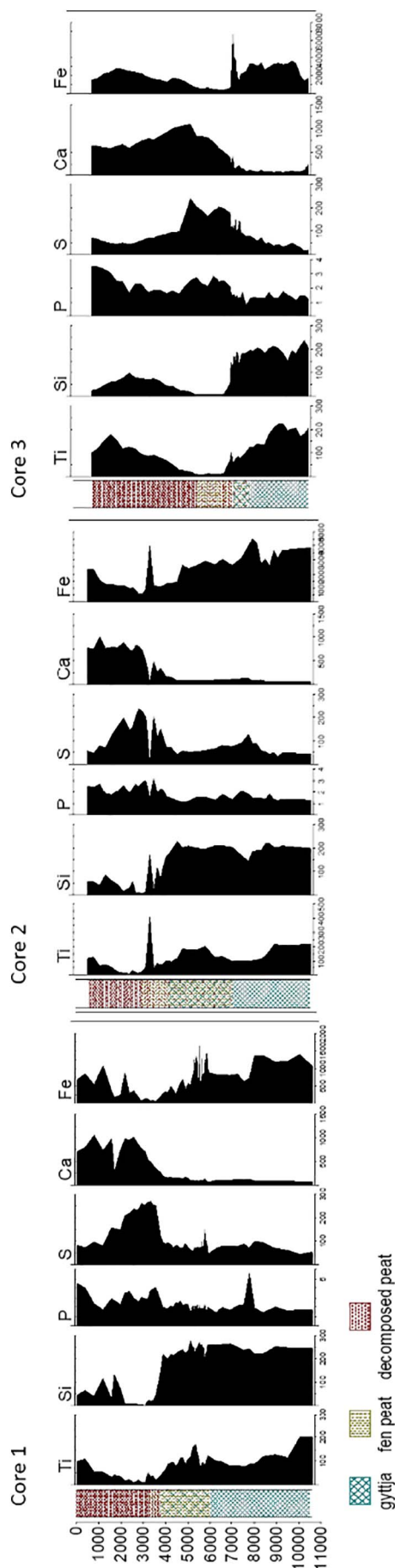


Fig. 2. Geochemical composition diagram of Cores 1, 2 and 3 plotted on the calibrated age scale (years B.P.).

4.3. Macrofossil record (Fig. 3)

Concentrations of plant macrofossils were not stable over time and differed between profiles. In Core 1, three peaks in macrofossil abundance occurred at 7800 (80/sample), 5100 (115/sample) and 4000 cal yr B.P. (56/sample); the last peak represented the point at which the lake was infilled (cf. Fig. 3). Similarly, the point of the lake's infilling was characterized by an even more distinct increase in macrofossil concentrations in Cores 2 and 3 (up to 323/sample). After the lake's terrestrialization, macrofossil concentrations were rather low. The uppermost parts of all cores (the last 2–3 thousand years) were characterized by a poor macrofossil record, probably due to high mineralization of the sediment below the alder stands, so only few macrofossils were preserved.

Early Holocene macrofossil assemblages did not differ very much between the profiles, because macrofossils of aquatic plants (*Potamogeton crispus*, *Trapa natans*, *Myriophyllum spicatum* and *Najas marina*) were dominant in the entire lake, indicating the presence of a large water body in the past. Fish remains were present in Cores 2 and 3 continually during the aquatic phase, but appeared later in Core 1 (ca 8400 cal yr B.P.). The absence of fish remains in basal samples of Core 1 could be the result of the small total amount of macrofossils and thus not related to a lack fish in the lake at the onset of the Holocene.

The beginning of the Middle Holocene was characterized by terrestrialization in Core 3 (ca 7200 cal yr B.P.), which is indicated by an increased LOI, the expansion of wetland species *Lycopus europaeus* and *Eupatorium cannabinum*, and the disappearance of fish remains. By contrast, Cores 1 and 2 indicate that the Middle Holocene contained macrofossils of aquatic plants (e.g. *Potamogeton crispus*, *Najas marina*, *Myriophyllum spicatum*). During the Middle Holocene the lake surface transformed into a spatial mosaic of several vegetation communities assigned to the different lake successional stages. In some places pools with aquatic macrophytes persisted, but in others wetland communities started to dominate. Towards the end of the Middle Holocene, abundances of aquatic plants *Zannichellia palustris* and *Chara* sp., Cladoceran ephippia and especially species indicative of exposed bottoms such as *Cyperus fuscus* increased substantially in both Cores 1 and 2, which indicate a gradual lowering of the water depth.

The final disappearance of the remaining permanent pools took place at the beginning of the Late Holocene around 4200 cal yr B.P., when aquatic species exhibit declines and LOI rapidly increases in Cores 1 and 2. After 4200 cal yr B.P., species indicative of wetlands and exposed bottoms, such as *Carex pseudocyperus*, *Lycopus europaeus* and *Chenopodium glaucum/rubrum*, appeared in Core 2. Macrofossils of *Chara* sp., *Najas marina* and *Zannichellia palustris* are still present until 2800 cal yr B.P., indicating the presence of periodic shallow pools during the Late Holocene in the area of Core 2.

4.4. Pollen record (Fig. 4)

The first half of the Early Holocene period is characterized by the dominance of *Pinus* pollen (50–60%) with low concentrations of deciduous tree pollen of *Betula* (up to 10%), *Alnus* (6%), *Quercus* (8%), *Corylus* (5%) and *Ulmus* (5%). *Pinus* pollen decrease in the Early Holocene, yet the timing differs among the cores; ca 9500 cal yr B.P. in Core 1, and ca 8850 cal yr B.P. in Cores 2 and 3. Simultaneously with the decrease in *Pinus* pollen was the increase in deciduous tree pollen, mostly *Alnus*, but also *Quercus* and *Corylus*. Thereafter the pollen record remained rather stable until the expansion of *Fagus* (> 15%) between 5500 (Core 2) and 5300 (Core 1) cal yr B.P. The abundance of *Carpinus* pollen (> 5%) started increase a little earlier, at 5000 cal yr B.P. in Core 1 and 4350 cal yr B.P. in Core 2. The pollen record of Core 3 terminates at 6800 cal yr B.P., while Cores 1 and 2 terminate at 3650 and 3200 cal yr B.P., respectively. In the upper parts of profiles, where the decomposed peat was accumulated, pollen was not analysed.

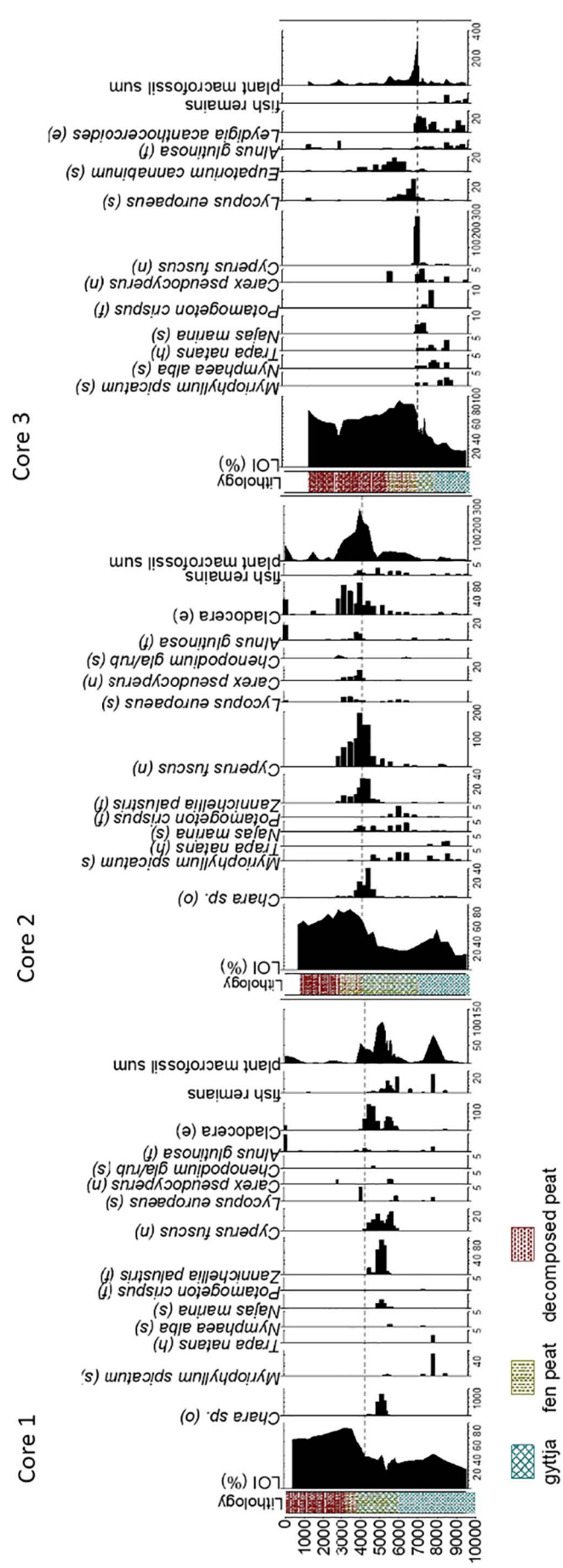


Fig. 3. Macrofossil concentration diagram of Cores 1, 2 and 3 plotted on the calibrated age scale (years B.P.). Numbers in 50 cm³ sediment. Percentage loss on ignition (550 °C) of the sediment is plotted. Dashed line indicates transition from standing water to periodical shallow pools or wetland. Abbreviations: e - ephippium, f - fruit, h - harpoon, n - nutlet, o - oospore, s - seed. For full macrofossil diagrams see Figs. S4, S5, S6 in the Supplementary data.

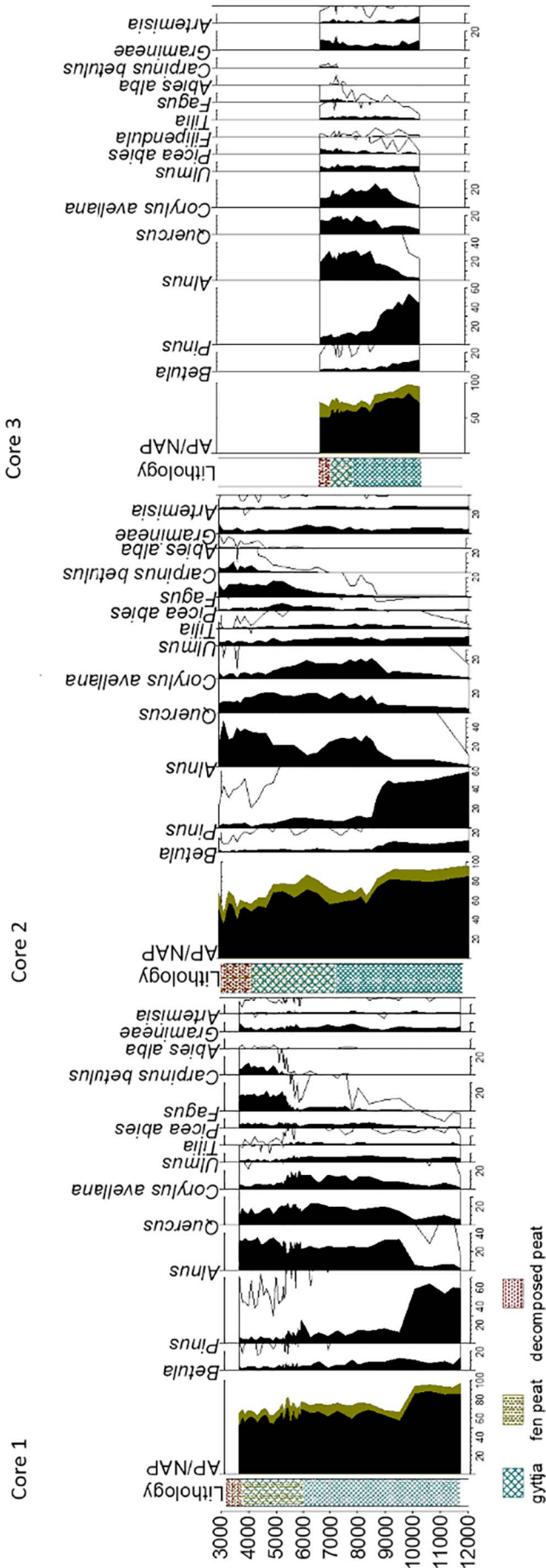


Fig. 4. Pollen percentage diagram of Cores 1, 2 and 3 plotted on the calibrated age scale (years B.P.). Yellow part of the AP/NAP ratio refers to non-arboreal pollen (NAP).

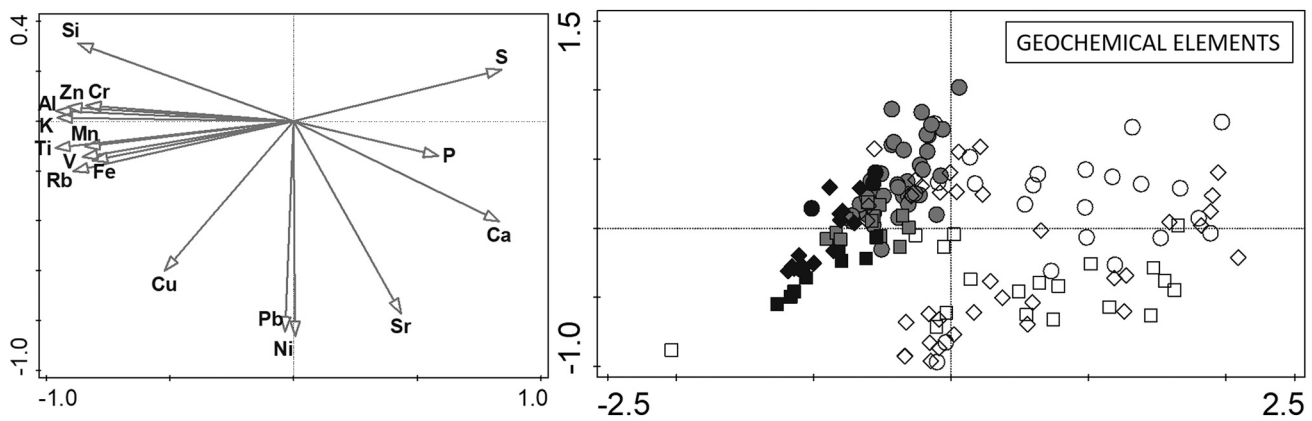


Fig. 5. NMDS (Euclidean distance, logarithmic transformation, data centered and standardized) of geochemical elements measured by EDXRF. Core 1 (circle), Core 2 (square), Core 3 (diamond); Early Holocene (black), Middle Holocene (grey), Late Holocene (white).

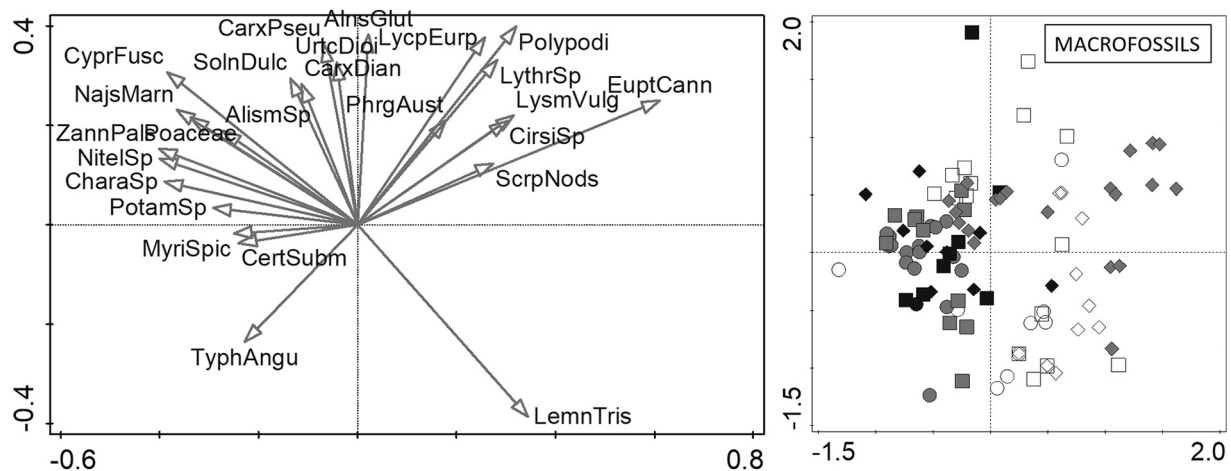


Fig. 6. NMDS (Hellinger distance, square-root transformation, centering and standardization by taxa) of macrofossil analysis. Core 1 (circle), Core 2 (square), Core 3 (diamond); Early Holocene (black), Middle Holocene (grey), Late Holocene (white).

Abbreviation: AlismSp – *Alisma* sp., AlnusGlut – *Alnus glutinosa*, CarxDian – *Carex diandra*, CarxPseu – *Carex pseudocyperus*, CertSubm – *Ceratophyllum submersum*, CharaSp – *Chara* sp., CirsiSp – *Cirsium* sp., CyprFusc – *Cyperus fuscus*, EuptCann – *Eupatorium cannabinum*, LemnTris – *Lemna trisulca*, LycopEurp – *Lycopus europaeus*, LysmVulg – *Lysimachia vulgaris*, LythrSp – *Lythrum* sp., MyriSpic – *Myriophyllum spicatum*, NajsMarn – *Najas marina*, NitelSp – *Nitella* sp., PhrgAust – *Phragmites australis*, Polypodi – *Polypodiophyta*, PotamSp – *Potamogeton* sp., ScrpNods – *Scrophularia nodosa*, SolnDulc – *Solanum dulcamara*, TyphAngu – *Typha angustifolia*, UrtcDioi – *Urtica dioica*, ZannPals – *Zannichellia palustris*.

4.5. Sources of variability of the palaeoecological record (Figs. 5, 6, 7, 8)

Differences among profiles were revealed also by the use of multivariate ordination methods, which is another way to visually see temporal and spatial changes in the palaeoecological record (Figs. 5, 6, 7). Analyses of macrofossil and geochemical data (Figs. 5 and 6) show that

Middle-Holocene samples from Core 3 are positioned among Late-Holocene samples from Cores 1 and 2 in the ordination space, indicating much earlier terrestrialization of Core 3 than of the other cores. All these samples are characterized by the occurrence of wetland species such as *Eupatorium cannabinum*, *Lysimachia vulgaris*, *Lythrum salicaria* and *Lycopus europaeus*, and by higher concentrations of Ca, S and P. The

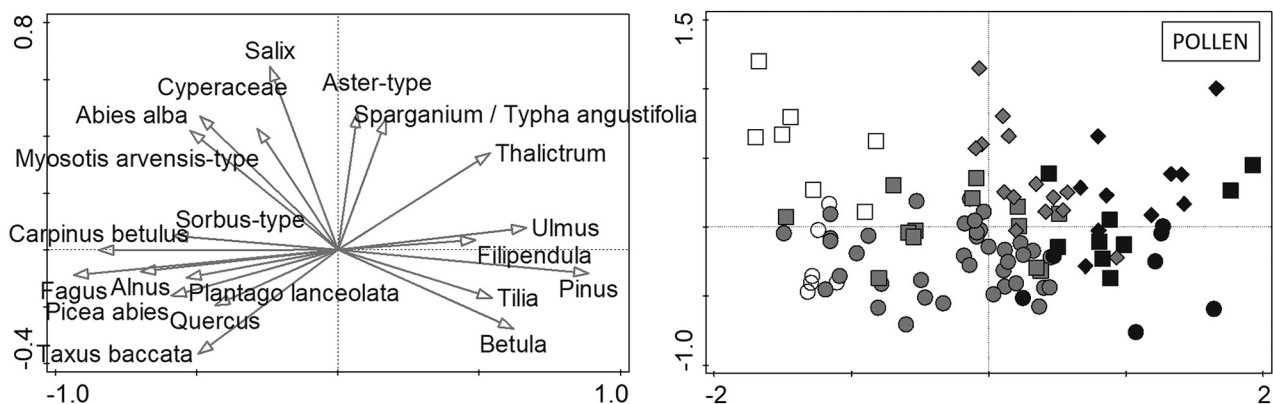


Fig. 7. NMDS (Hellinger distance, square-root transformation, centering and standardization by taxa) of pollen analysis. Core 1 (circle), Core 2 (square), Core 3 (diamond); Early Holocene (black), Middle Holocene (grey), Late Holocene (white).

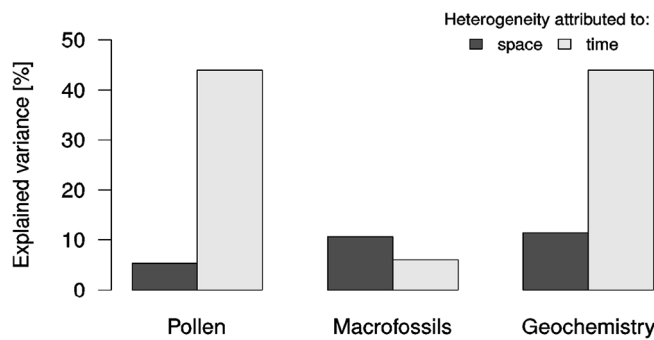


Fig. 8. Amount of variance in the data that could be attributed to spatial (differences among cores - dark bars) and temporal (changes over time — light bars) heterogeneities. Bars represent adjusted R^2 values for the respective aspect and type of data.

different timing of the lake terrestrialization was not reflected in the pollen spectra at all, and all Middle-Holocene samples are positioned together in the middle part of the ordination space (Fig. 7).

Variance partitioning illustrates the role of time and space in the variability of the geochemical, macrofossil and pollen data (Fig. 8). Overall, 47.1% of the variability in the pollen data could be attributed to both to the temporal dynamics of the fossil pollen record and differences among cores. Variability among cores was estimated at 5.3% whereas variability that could be ascribed to temporal dynamics reached 44%. Please note that the reported values are adjusted to the degrees of freedom of the data and therefore do not have to sum up to the overall value. Using geochemical data, 53.4% of the variability could be attributed to both spatial and temporal differences. Variability among cores was estimated at 11.4%; temporal variability was estimated at 44%. For the macrofossil data, the pattern was opposite with only 15.7% of the overall variance being attributable to spatiotemporal heterogeneity; the net effect of the spatial component was 10.6%, and the net effect of the temporal dynamics was only 6%.

5. Discussion

5.1. Water-depth fluctuations and long-term local vegetation development

Water chemistry and nutrient status are the most important local factors affecting the structure and composition of lake and shore vegetation (Hannon and Gaillard, 1997). The presence of nutrient-demanding plant species (e.g. *Trapa natans* and *Potamogeton crispus*) indicates that the water was the most probably eutrophic during the Holocene in palaeolake Šúr (Chytrý, 2011). Such eutrophic lowland lakes are characterized by rich lake-shore vegetation communities and well developed belts of submerged, floating-leaved and emergent aquatic plants. Because each aquatic plant is related to a particular range of water depth, we can estimate water depth changes based on the presence of each aquatic assemblage (Hannon and Gaillard, 1997). For example, submerged and floating-leaved aquatic plants (*Myriophyllum spicatum*, *Potamogeton crispus*, *Najas marina*, *Trapa natans*, *Nymphaea alba*; alliance *Potamion* Miljan 1933 and *Nymphaeion albae* Oberdorfer) dominated in the macrofossil record of the Early Holocene. According to Hannon and Gaillard (1997), *Trapa natans* and *Nymphaea alba* have an optimum of occurrence in the depth range of 100–200 cm and 100–150 cm, respectively, which indicates that the water column was higher than 100 cm. The continuous gyttja layer deposited throughout the whole basin suggests the existence of an extensive shallow lake at that time (Danišovič et al., 1956) (Fig. 1).

Macrophytes belonging to the alliances *Potamion* and *Nymphaeion albae* (e.g. *Najas marina*, *Najas minor*, *Nymphaea alba*, *Potamogeton* spp. and *Chara* sp.) also prevailed in the Vracov lake (southern Moravia) during the Early Holocene, which also suggests a high water depth (Rybničková and Rybniček, 1972; Potůčková, unpublished data).

At the beginning of the Middle Holocene, *Najas marina* (alliance *Potamion* Miljan 1933) and *Cyperus fuscus* (alliance *Eleocharition ovatae* Philipi 1968) prevailed near center of palaeolake Šúr (Core 3) indicating a lowering of the water depth. *Najas marina* prefers shallower water, optimum depth range of 0–100 cm (Hannon and Gaillard, 1997), whereas *Cyperus fuscus* grows in disturbed places as the result of a lowering in water level (Chytrý, 2011). Subsequent to the decrease in water depths was the appearance of wetland plants *Lycopus europaeus* (class *Phragmito-Magno-Caricetea* Klika in Klika et Novák 1941) and *Eupatorium cannabinum*. The presence of these particular wetland plants together with a shift from gyttja to marsh peat indicate the formation of a terrestrial island near the center of the lake (Core 3) at 7200 cal yr B.P. Additionally, the presence of *Cyperus fuscus* and *Chenopodium glaucum/rubrum* (alliance *Chenopodium rubri* Tüxen 1960) during the Middle Holocene in Cores 1 and 2 also implies a lowering of the water depth (Watts and Winter, 1966; Birks, 1973; Wasylkowa, 2005).

Climate is one of the most important factors affecting water level changes (Harrison et al., 1993). During the Middle Holocene a dry climate prevailed in the Danubian Lowland (Jamrichová et al., 2014), which possibly caused desiccation of water bodies. For instance, the expansion of reed beds suggests a drop in water level in lake Balaton around 7000 cal yr B.P. (Sümegi et al., 2008). However, no significant limnologic changes or changes in macrofossil record in Core 1 and 2 (i.e., the expansion of wetland species) were recorded at palaeolake Šúr during the Middle Holocene, suggesting that the lake did not dry out. Because the water supply of palaeolake Šúr was originally from streams flowing from the Little Carpathians, one can speculate that snow accumulation and subsequent melt-water was affected negligibly by the drier conditions seen during the Middle Holocene. However, we cannot exclude that the water level slightly decreased during the Middle Holocene.

Lowering of the water depth in palaeolake Šúr was driven mostly by the gradual accumulation of organic matter at the bottom of the lake. The predominance of high biomass producing macrophytes *Trapa natans* and *Nymphaea alba* may accelerate the process of infilling (Chytrý, 2011), which may have led into earlier terrestrialization of Core 3. Together, the results from the three different cores document a patchy mosaic of various vegetation associated with distinct successive stages of terrestrialization as water depth decreased during the Middle Holocene, highlighting that changes in water depth were not homogenous, but rather heterogeneous in space and time.

Similarly, the macrofossil record from Lake Zeribar (Iran) indicates that in some periods in the past, the aquatic and mire plant successions were rather synchronous in the whole lake, while in the other phases were horizontally differentiated (Wasylkowa and Walanus, 2004; Wasylkowa, 2005). The same scenario was documented in a complex of lakes and bogs in northeastern Poland in the Suwalski Landscape Park (Gałka and Apolinarska, 2014; Gałka, 2014).

Terrestrialization of the studied part of lake basin occurred ca 4200 cal yr B.P., according to Cores 1 and 2, when macrofossils of aquatic plants started to decline and wetland plants increased. However, periodic shallow pools were present near Core 2, with aquatic plants tolerating short-term desiccation (*Zannichellia palustris* and *Chara* sp.) even until 2800 cal yr B.P. (Chytrý, 2011). After the infilling of different parts of the lake by organic matter, the first marsh vegetation expanded but was subsequently displaced by an alder carr (*Alnion glutinosae* Malcuit 1929). This occurred at the site until today and is treated as the final succession stage of eutrophic lakes (Hannon and Gaillard, 1997). Alder roots aerate organic substrate and consequently mineralization process occurs, which led to decomposition of organic material and subfossil remains in the upper part of the sediment (Barthelmes et al., 2006; Prager et al., 2012).

5.2. Regional vegetation development

In the Early Holocene, *Pinus* percentages decreased simultaneous

with decreases in Ti, however, the timing varied between cores; 9500 cal yr B.P. in Core 1, and 8850 cal yr B.P. in Cores 2 and 3. The amount of the lithogenic Ti indicates the input of clastic material into the lake, which suggests an unstable soil cover around the lake (Oldfield et al., 2003). The decline in Ti in our record likely reflects the displacement of *Pinus* by deciduous trees, which typically have more continuous plant cover and more stable soils than landscapes covered by *Pinus*. The time discrepancy between the *Pinus* and Ti decrease among profiles is the most probably caused by inaccurate radiocarbon dating of Core 1 in the lower part of the profile (Table 1). Another possible explanation is the position of the cores, because Core 1 is on the edge of the basin and could reflect the environment in the vicinity of the lake better. The rapid decline of *Pinus* was further followed by an increase of temperate trees (*Quercus*, *Corylus*, *Alnus*) whereas the pollen percentages of the Gramineae and *Artemisia* record did not change. Hájková et al. (2013) also document a similar change in vegetation composition, around 9500 cal yr B.P. in the Nitra Basin, situated ca 100 km to the northeast of the Šúr locality. The regional increase in deciduous trees is likely linked with climate amelioration after 9500 cal yr B.P., as suggested by a macrophysical model for the Danubian Lowland (for details see Jamrichová et al., 2014). However, at the other site Nad Šenkárkou (560 m a.s.l.), which is located in Malé Karpaty Mts. ca 10 km to the northwest of the Šúr locality, the change from *Pinus* to *Corylus* occurred ca 1000 years earlier (around 10,500 cal yr B.P.) (Gálová et al., 2016). The earlier expansion of deciduous trees at Nad Šenkárkou could be attributed to either differences in local climate conditions (mountains/lowland) or by the surrounding bedrock/substrate because the palaeolake Šúr is situated on fluvial sands and gravels in the lowland, which favoured the dominance of *Pinus*, whereas the site Nad Šenkárkou is situated on crystalline bedrock in the mountain range. The decline in *Pinus* was evident even later (ca 5000 cal yr B.P.) in southern Moravia, which may be linked with widespread sandy soils, dry climatic conditions or both (Kuneš et al., 2015).

The expansion of *Fagus* took place between 5500 and 5300 cal yr B.P., as illustrated in Cores 1 and 2. This is in agreement with other sites near palaeolake Šúr, which document the expansion of *Fagus* beginning between 5500 cal yr B.P. (Malé Bielice; Hájková et al., 2013) and 5850 cal yr B.P. (Nad Šenkárkou; Gálová et al., 2016). The expansion of *Carpinus* occurred later at 5000 (Core 1) and 4350 cal yr B.P. (Core 2), which is in agreement with the timing of *Carpinus* expansion at Malé Bielice around 4600 cal yr B.P. The time discrepancy of *Carpinus* expansion among Cores 1 and 2 is likely explained by the position of the cores, as dispersion and deposition of pollen grains could be influenced by advanced lake fragmentation process, water flow or by accumulation of pollen near the shore. However, as previously mentioned, the discrepancy could be related to inaccurate radiocarbon dating.

5.3. Sources of variability of the palaeoecological record

Despite discrepancies among the cores mentioned above (e.g. *Pinus* and Ti decline), the spatial dynamics of the pollen record are still very low and explain 5.3% of variability (Fig. 8). Variability that could be ascribed to temporal dynamics reached 44% of the variability in the pollen data. Temporal variability reflects the arrival, expansion and retreat of pollen taxa over time. Low spatial variability is likely the result of larger lakes basins having relatively large pollen source areas that reflect regional vegetation (Bradshaw and Webb, 1985; Jacobson and Bradshaw, 1981; Jackson, 1990). Therefore, pollen records from several cores from one basin tend to exhibit a low degree of the heterogeneity (Demske et al., 2005; Lotter et al., 1992). Wind-induced mixing of the water column, as well as autumn and spring circulation (which is very intense in shallow lakes) contributes to the homogenization of pollen fallout deposited in the sediment (Lampert and Sommer, 2007). Additionally, all three cores were taken from the

deepest part of the lake, which is another possible reason of the rather low spatial variability. Despite very low spatial dynamics, we demonstrate different timing of retreat/expansion of several taxa among cores. However, low-resolution sampling and inaccurate radiocarbon dating disable us to derive explicit conclusions about causes of this discrepancy.

The spatial and temporal heterogeneity of the macrofossil record explains 10.6% and 6% of the variability, respectively (Fig. 8). The low values characterizing temporal and spatial dynamics could be influenced by a fragmentary record stemming from poor macrofossil preservation (Birks, 1980). However, the macrofossil record in the sediment of the palaeolake Šúr was well preserved. The low temporal variability is thus a result of a slow local vegetation development. Water acts as a buffer against many external environmental fluctuations, making lake ecosystems more constant (Szafer, 1954; Lampert and Sommer, 2007), which contributes to the stability of macrophyte communities over millennia (Gałka et al., 2014; Rasmussen and Anderson, 2005). High species turnover (which contributes to higher temporal variability) occurs predominantly during the lake successional stage from a lake environment to a marsh (Rybníček and Rybníček, 1972; Gálová et al., 2016). Another source of rapid species turnover in aquatic communities is anthropogenic eutrophication, which reduces the species diversity of macrophytes in naturally mesotrophic or eutrophic shallow lakes (Egertson et al., 2004; Jeppesen et al., 2000; Sayer et al., 2010). However, during the time interval under study, 10,500–7000 cal yr B.P., the composition of aquatic species was mostly stable with low species turnover during the Early Holocene and only one lake/marsh transition recorded in Core 3 around 7200 cal yr B.P., leading to low temporal variability. The position of cores explains roughly 5% more of the spatial variability when compared to pollen, which is a result of aquatic plant patchiness and local dispersion of seeds (Zhao et al., 2006; Greathouse, 1983).

Sedimentological and geochemical characteristics of sediments reflect both local and regional signals (Fig. 8). For example, there appears to be a connection with the local development, which is mainly associated with autogenic succession of the lake. This is illustrated by the termination of gyttja accumulation in association with the decline of Si and the disappearance of diatoms. On the other hand, higher concentrations of lithogenic elements (e.g. Ti) indicate erosion processes the lake catchment and thus reflect the regional environment (Oldfield et al., 2003). The geochemical composition of the lake sediments appears to be very sensitively to changes in both local and regional environment, which made this variable very dynamic over time (44% variability explained). The geochemical elements under study are correlated with the type of sediment, meaning that changes in sediment type result in changes in geochemical signal. Unequal accumulation rates of sediments at the bottoms of lakes leads to spatial patchiness of sediments and associated elements (Dearing, 1997), which corresponds with the higher amount of variability (11.4%) explained by space in comparison to pollen data. However, rather low spatial variability of geochemical and macrofossil data is given by the fact, that all three cores were taken from the deepest part of the lake and only several hundred meters from each other.

6. Conclusions

Hydroseral succession in the palaeolake Šúr exhibits a typical course of lowland lake vegetation development recorded by a shift from the dominance of submerged and floating-leaved plants (alliance *Potamion* and *Nymphaeion*), through the dominance of wetland species (class *Phragmites-Magno-Caricetea*) to the final expansion of an alder carr (alliance *Alnion glutinosae*). Vegetation succession was affected by gradual sediment accumulation and by long-term natural eutrophication of the lake during the Holocene. During the Middle Holocene, different sediment accumulation rates caused the lake surface to become a spatial mosaic for several vegetation successional stages connected with a

particular phase of the infilling process (and water depth) during the Middle Holocene. Such spatial heterogeneity of local vegetation succession, recorded in extensive but rather shallow lakes, points to the necessity to investigate core series when reconstructing past local lake development using macrofossil analysis. The pollen record, by contrast, reflects the surrounding vegetation on a broad scale very well, as it is less dependent on the environment within the lake. However, additional high-resolution and well radiocarbon dated investigation of core series is essential to determine possible causes of different timing of dominant pollen taxa expansion or retreat in different parts of the lake basin.

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Appendix A. Supplementary data

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